Female Soay sheep do not adjust their maternal care behavior to the quality of their home range

Title: **Female Soay sheep do not adjust their maternal care behavior to the quality of their home range**

Running title: Does home range quality influence maternal care?

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Abstract

Resource availability, through its impact on the costs and benefits of parental care, is expected to influence parental care behavior. There has, to our knowledge, been no attempt to understand how variation in the resource use of wild individuals influences individual parental care behavior. To understand how natural resource variability affects maternal care in female St. Kilda Soay sheep, we selected 69 females whose home ranges varied in quality (measured as the mean percentage cover of *Holcus lanatus*), and recorded the behavior of each individual and her lamb over the period of maternal

care. Home range quality did not influence suckling or non-suckling behaviors of the female or her lamb, suggesting that maternal care did not vary with a female's access to resources. Growth rate analyses confirmed the behavioral results, with no association between home range quality and the weight gain of lambs between birth and weaning. This work suggests that female Soay sheep faced with poorer resources do not favor their own future success over that of their lamb, and thereby do not exhibit a conservative reproductive strategy. This may be because when resource levels are high during the summer, females are able to offset the costs of lactation by consuming additional resources, regardless of the location of their home range. Our results suggest that more studies characterizing the environment experienced by individual animals will be necessary to fully understand how individuals alter their behavior in response to temporal and spatial variation in the environment.

Key words: Soay sheep, maternal care, home range quality, resource availability, wild, ungulate

Introduction

Parents of many species provide their offspring with parental care, which can be defined as any parental trait that increases the fitness of the offspring, and that originated for or is currently maintained for this purpose (Smiseth et al. 2012). Providing care often comes at a cost to the parent's own survival and future reproduction, at which point it can be termed parental investment (Smiseth et al. 2012). To maximize their own lifetime reproductive success, parents must balance the benefits of investing in current offspring against the costs of reduced future reproductive opportunities. As a result, parents are expected to adjust the level of care they provide to the benefits of care to their offspring and the cost to themselves (Winkler 1987). Many factors have the potential to influence the relative costs and benefits of parental care thereby contributing to variation in the level of parental care. These factors can relate to the offspring themselves, for example their relatedness to the parent (Møller and Birkhead 1993; Dixon et al. 1994) or their sex (Hasselquist and Kempenaers 2002). Similarly, in species where care is shared among multiple individuals, the benefit can vary depending on the amount of care provided by the focal parent as well the amount provided by its partner (Lessells 2012) or any helpers (MacColl and Hatchwell 2003). The environmental conditions that a parent experiences can also alter the benefits of care to offspring and/or the costs of providing care to the parent, and thereby influence the level of parental care provided (Clutton-Brock 1991).

The environment an individual experiences is complex, composed of a wide variety of biotic and abiotic factors. Research has shown that parental care behaviors are influenced by an array of environmental components, from predation risk (Fontaine and Martin 2006; Huang and Wang 2009) and the social environment (Bales et al. 2002; Russell et al. 2008; Brouwer et al. 2014) to weather conditions (Thierry et al. 2013; Öberg et al. 2015) and resource availability (Scornavacca et al. 2016). Much of the literature on the effects of environmental variation has focused on resource availability, which is unsurprising given that resource availability dictates the amount of energy that is available for growth, survival, or reproduction. However, empirical work is yet to uncover a consistent relationship between resource variability and parental care. Many studies report no influence of resource availability on parental care decisions (e.g. Whittingham and Robertson 1994, Andrews et al. 2016), whilst other studies find reductions (e.g. Whittingham and Robertson 1994), or increases in parental care with increased resource availability (e.g. Rachlow and Bowyer 1994; Wong and Kölliker 2012; Markman et al. 2002). The diversity evident in the existing literature may derive from differences in the effect of resource variation on the survival and reproductive value of adults versus offspring (Clutton-Brock

1991). Decreased resource availability is expected to result in increased parental care if the parent's potential for reproduction in the future is low relative to that of the offspring (Clutton-Brock 1991). However, if future reproduction of the parent is less affected by resource scarcity than the future reproduction of the offspring, then a decrease in resource availability should be associated with reductions in care because parents should favor their own future reproduction (Clutton-Brock 1991). This argument suggests that the effect of resource variation on parental care is linked closely with life history. For example, females of long-lived iteroparous species, such as ungulates, might adopt a conservative reproductive strategy, such that when faced with resource scarcity they allocate fewer resources to their offspring and maintain their own condition (Martin and Festa-Bianchet 2010). This is because their fitness is more dependent on their own survival than their reproductive success in any single year (Gaillard and Yoccoz 2003).

Despite the long-established interest in the effect of resource availability on parental care, there are still substantial gaps in our understanding. First, much of the previous research has utilized bird systems. Most birds have bi-parental care (Clutton-Brock 1991), which is a rare pattern of care in most other taxa, including mammals. In most non-avian taxa, a single parent (usually the female) provides all care to the offspring (Stahlschmidt 2011). Where both parents provision the offspring, the response of one parent to environmental conditions may be conditional on the behavior of the other parent (Lessells 2012), which could make it difficult to detect an association between environmental conditions and parental care. Second, supplementation experiments are commonly used to understand how resource availability affects parental care. Such experiments might come at a cost in terms of loss of biological realism and therefore it may be beneficial to complement the use of experimental manipulations with studies using natural variation in resources. Third, the limited number of studies on naturally occurring variation in resources in wild populations are often based on comparisons between different populations (e.g. Tremblay et al. 2004). This practice is problematic because it is difficult to separate the effects of environmental conditions from behavioral differences between populations due to genetic differentiation (Johannesson and Johannesson 1996). Fourth, care must be taken to quantify environmental conditions in a way that accurately reflects its impact on the study organism. Much of the literature has focused on the effect of between-year variation in resource availability on parental investment, using population density and/or mortality as a proxy for resource availability (e.g. Robertson et al. 1992). This approach does not account for the fact that individuals are more likely to respond to the resource levels they experience in their home range than to the resources available

to the population as a whole. Movement ecologists have developed sophisticated methods to estimate individual space use (e.g. kernel density home range estimators), making it possible to examine the effects of fine-scale resource variation on individual parental care decisions. However, to our knowledge, these approaches have not been used to study the effect of resource variation on parental care. Finally, studies tend not to record the behavior of the offspring. However, any influence of environmental conditions on offspring behavior may influence the parent's behavior, thereby potentially influencing any relationship between parental behavior and environmental variation such as resource availability.

The St. Kilda population of Soay sheep is an ideal system in which to study the effect of resource variation on parental care behavior. The long term data available (Clutton-Brock et al. 2004) make it possible to quantify both between-individual and between-year variation in environmental conditions. Furthermore, individuals are marked with unique ear tags, making it possible to record the behaviors of specific females and their lambs. Body weight is associated with many aspects of female reproduction and survival in Soay sheep, influencing the probability of conception in the first year, the likelihood that females bear twins, and the probability of over-winter survival (Clutton-Brock et al. 2004). A female's body weight is also closely tied to the birth weight of her lambs (Clutton-Brock et al. 2004), which in turn affects their early survival (Jones et al. 2005). Body weight and condition are likely to be closely related to home range quality, and there is marked variation in forage quality and quantity across the study area (Coulson et al. 1999; Regan et al. 2016). *Holcus-Agrostis* (HA) grassland is the most productive plant community on the island (as determined using grazing exclosures), containing the highest live standing-crop biomass (Crawley et al. 2004). This community is also highly palatable to the sheep, with sheep selecting for this community even at high density (Jones et al. 2006). The aim of this study is to understand how natural variation in resource availability affects patterns of maternal care in female St. Kilda Soay sheep (*Ovis aries*). To this end, we studied the parental behavior of females and the sucking behavior of their lambs over the period of maternal care in 2014 and 2015. We selected females based on the quality of their home range, measured as the mean percentage cover of *Holcus lanatus* (one of the dominant species in *Holcus-Agrostis* grassland) within their core home range, before following them in the field after the birth of their lambs in April/May until weaning in August.

Methods

Study population

Soay sheep were introduced to the island of Hirta in 1932 from the neighboring island of Soay in the St. Kilda archipelago, Scotland (57°49° N 08°34° W). Since their introduction they have been entirely unmanaged, and the total island population now ranges from 700 to 2300 individuals, depending on variation in mortality between years. Hirta's sheep have been studied since the early 1960s, but intensive study of the Village Bay population (containing ∼30% of the total island population) commenced in 1985. To enable identification individual sheep are marked with plastic ear tags shortly after birth and within the Village Bay area more than 95% of animals are tagged (Clutton-Brock et al. 2004). A combination of mortality checks and censuses enable the monitoring of individual survival, whilst also providing information on individual space use. Female Soay sheep are philopatric, with more than 80% remaining in their natal heft throughout their life (Coltman et al. 2003). Given the home range fidelity exhibited by female Soay sheep and the substantial spatial heterogeneity in grazing quality across the study area, individuals vary in their access to resources (Regan et al. 2016) and consequently will likely vary in their reproductive investment decisions.

Home range estimation and animal selection

Researchers from the Soay sheep project travel to St. Kilda three times per year (April-May, July-August, October-November), and conduct ten censuses of the Village Bay area during each trip. During each census, three fixed routes are walked simultaneously and the identity and grid reference (to the nearest 100 meters) of all encountered individuals is noted. In the Spring of 2014 and 2015, we extracted census observations for all females that were recorded as being alive in the preceding census, were aged between 3 and 8 years (to exclude young and geriatric individuals due to likely differences in their behavior), and that had at least 49 census observations in total. This is because 49 observations is the minimum number needed to reach an asymptote in core home range area when estimating lifetime home ranges, indicating that the core home range has been reliably estimated (see Regan et al. 2016 for details). We transformed these observations onto a grid, so that the most south-westerly census observation (NF091980) became (0,0) and each step on the grid represented a distance of 100 meters. Because the census procedure means that animals are assigned a grid reference to the nearest 100 meters, individuals frequently have numerous observations with identical grid references.

This can cause problems when estimating home ranges using kernel methods (Tufto et al. 1996) and we therefore added a random number between -20 and 20 (representing a distance of up to 20 meters) to both the X and Y coordinates of each observation before home range estimation (see Moyes 2007 ; Stopher et al. 2012).

Home ranges were calculated using census observations from all years of a female's life prior to the observation period to maximize the number of potential study animals, and also because data were not yet available at the time of animal selection for all censuses in the year preceding observation (we have since conducted analyses using annual home range estimates/resource selection functions - see below for details). We estimated core home ranges (70% isopleth; see Regan et al. 2016 for details) using kernel density methods with the package 'adehabitatHR' (Calenge 2006) in R version 3.1.3 (R Development Core Team 2008). Use of the reference bandwidth (h_{ref}) can result in over-smoothing and consequently biased home range estimates, leading Kie (2013) to suggest a rule-based *ad hoc* method for estimating the bandwidth. This method involves sequentially reducing h_{ref} until the 95% kernel home range polygon fragments or lacuna appear, at which point the process is stopped (Kie 2013). We estimated home ranges using both methods, finding that in many cases the home range was already fragmented when using h_{ref}, preventing any further reduction in the smoothing parameter, and that the use of the *ad hoc* bandwidth, where possible, had very little impact on estimates of the percentage cover of *H. lanatus*, and therefore did not change our results. As a result, we present analyses using home ranges calculated using h_{ref}. Though data from both 2014 and 2015 field seasons could be used for the analyses described below it must be noted that, in 2014, females were selected specifically based on their access to resources (see below), whereas in 2015 their home ranges were calculated to enable us to account for space use when selecting females based on the predicted growth of their lambs.

We quantified the variation in home range quality by characterizing the vegetation present within each individual's home range. Using the Ordnance Survey Grid, the Village Bay study area is divided into 160 one hectare squares (100 × 100 m) [the remaining 10 hectares were not surveyed for vegetation due to access difficulties and/or a lack of vegetation (some are covered by scree)]. Between 2008 and 2012 complete species lists were compiled for the vascular plants in each hectare, and the percentage cover of each species (to the nearest 5%) was scored by eye. MJC collected all botanical data so there were no between-observer sources of error. Ocular cover estimation is the only practical method for hectare-sized plots because it averages over the within-plot spatial heterogeneity. Furthermore, calibrations of visual cover estimates against biomass data in related studies has shown that the

results from the two methods are strongly correlated (e.g. Allan and Crawley 2011, MJC, unpublished analysis). Plant community boundaries are the same as described in Gwynne et al. (1974), and there has been no detectable change in the botanical composition of these communities since detailed botanical recording began in 1993 (MJC, unpublished results). We obtained home range quality metrics by calculating the percentage cover of *H. lanatus* in individual core home ranges. We did this by taking a weighted mean of the percentage covers recorded in the hectares contained within each individual's home range. The proportion of the hectare contained within the home range was used as a weight to ensure that the varying contributions of constituent hectares was taken into account.

Upon completion of both field seasons, we estimated home range quality metrics and individual resource selection functions for the year preceding behavioral observation. We focused on the year preceding observation for two reasons. First, it was not possible to assess individual space use for the precise period in which behavioral observations were conducted because space use data are only collected three times per year (April, August, and October). Therefore, to incorporate data from the April directly preceding the birth of the lamb, whilst having enough data to estimate home ranges, we used spatial data from the four census periods (April-April) preceding the observations. Second, the resources available to a female prior to lactation are likely to influence her body weight or condition and therefore may also affect her provisioning over the maternal care period (Landete-Castillejos et al. 2003). We used annual home range quality and resource selection functions to provide a more complete picture of the relationship between resource availability and maternal care by enabling us to characterize variation in access to a wider range of plant communities and making it possible to assess the impact of characterizing home range quality at a particular temporal scale. We estimated annual home ranges and home range quality metrics for each individual in the same way as the lifetime home ranges, but using only location data from the four census periods (April-April) preceding the time of observation. Because using the mean percentage cover of *H. lanatus* as a measure of home range quality may be sensitive to variation in home range size we calculated an alternative measure of quality for annual home ranges in order to assess the robustness of our results. We weighted the percentage cover of *H. lanatus* in each hectare covered by an individual's utilization distribution (70% isopleth) by the amount of the hectare contained within the utilization distribution before summing these values to give an estimate of the area of an individual's home range that was covered by *H. lanatus*.

We also estimated individual resource selection functions for the year before each field season in order to obtain a more thorough measure of an individual's use of habitat. Resource selection

functions (RSFs) estimate habitat selection by comparing the characteristics of locations used by organisms against those not used (Manly et al. 2002); however, because we are unable to explicitly ascribe absences to locations, our data correspond to a used/available design (Boyce et al. 2002). By using RSFs, we could characterize each individual's selection for multiple plant communities, including HA grassland. We estimated second-order habitat selection; that is, the selection of the home range (Johnson 1980), as this most closely corresponds to the home range quality measures described above. We sampled n used locations directly from the 95% kernel annual home range contour (calculated as above), whilst n available locations were sampled randomly from the area covered by the 160 hectares for which there are vegetation data (n was the number of census observations for each individual over the April-April preceding observation). To make use of percentage cover data for the fourteen most common plant species, but reduce the number of variables included in the RSF, we used principle components analysis to derive three variables (the first three principal components [PC1, PC2 and PC3] which accounted for 59.3% of the variation across hectares). PC1 loaded negatively on species present in *HA* grassland (including *H. lanatus*, *Agrostis capillaris* and *Festuca rubra*) and in the maritime *Festuca-Plantago* swards (including *Plantago lanceolata* and *P.maritima*) and positively on species associated with heathland, including *Calluna vulgaris* and *Nardus stricta* (see Fig. S2). In contrast, PC2 loaded positively on species associated with HA grassland and negatively on species associated with *Festuca-Plantago* swards, whilst PC3 loaded positively on *Calluna vulgaris* (see Fig. S3). We calculated an RSF for each female using the three principal components as predictors in a logistic regression (Manly et al. 2002). We then extracted the coefficients from these regressions for use in subsequent models aimed at understanding how variation in resource selection was associated with variation in maternal care behaviors (see below).

Behavioural observations

We successfully tracked 34 females in 2014 and 35 females in 2015 (females were never observed in both years), all of which gave birth to singleton lambs. We focused on singletons because low twinning rates in both years (2014 - 18%, 2015 - 12%) meant that it was unlikely that we would be able to follow enough twins to enable us to detect any difference in the response of females to resource variation as a result of differences in litter size. The females varied substantially in the quality of their home ranges, with the mean percentage cover of *H. lanatus* in lifetime home ranges ranging from 9.6% to 61.5%. To monitor the behavior of females and their lambs from birth until weaning, we made three trips to

St. Kilda each year. The first started in mid-April and lasted until late May (2014 - 15/04 to 28/05, 2015 - 13/04 to 21/05), the second trip occurred in June (2014 - 23/06 to 02/07, 2015 - 23/06 to 05/07) and the final trip commenced in late July (2014 - 22/07 to 04/08, 2015 - 22/07 to 03/08). Focal observations were conducted once for each week of the lamb's life where possible (see Fig. S1 for an illustration of observation spread for each individual) using 'Animal Behaviour Pro' (Newton-Fisher 2012). One female (BR501) and her lamb died shortly after the second observation was conducted; however, the inclusion of data for this pair did not modify the results and, therefore, we present results with these data included. Individuals were located using 10x42 binoculars (Vortex, USA) and spotting scopes (16-48x; Opticron, UK), and were then observed from a distance of at least ten meters. It was not possible for observations to be done totally blind because animals were specifically selected based on their home range quality and because there are visible differences in the vegetation across the study area; however, assistants had limited information regarding the home range quality of different animals and the quality of different communities within Village Bay. Observations were conducted between 08:00 and 19:00, and the focal watches for each individual were distributed across the day and between observers (2 per trip) to prevent any between-individual differences caused by the data collection procedure. Focal observations lasted one hour, with lamb behavior recorded continuously and female behavior recorded instantaneously at two minute intervals (see Table 1 for descriptions of the recorded behaviors). Whenever females and lambs separated, we preferentially kept the lamb in sight in order to accurately record non-sucking behaviors. Hirta is littered with dry-stone structures known as cleits, which were used for storage by the St. Kildans, but are now used for shelter by the sheep. Sheep are very difficult to observe when inside a cleit, and we therefore ended observations when both the female and her lamb entered a cleit. We continued with observations when either the female or her lamb were inside a cleit, recording them as 'Out of sight', as in this case we could be sure that no suckling events were missed. There was one case where a lamb sucked from both its mother and grandmother and in this case we recorded, but later excluded, all sucks from the grandmother prior to analysis. In total, we conducted 570 hours of observations, with between two and thirteen focal watches per female-lamb pair (Fig. S1).

Statistical analyses

For each focal observation, we calculated suckling frequency (the number of suckling events per hour regardless of length), total sucking time (the total time in seconds that a lamb spent sucking per

hour), and the mean suckle duration (total sucking time divided by the frequency of suckling events). One suckling event which lasted 248 seconds was removed as it was a clear outlier, having likely been extended due to vigilance in response to tourist disturbance. We also calculated the frequency of failed suckling events, denoted as a suckling bout shorter than five seconds (following Hass 1990; Birgersson and Ekvall 1994; Tollefson et al. 2011) (the number of failed suckling events per hour), the frequency of female terminated suckling events (the number of suckling events terminated by the females per hour), and the total time (in seconds) that a lamb spent grazing, playing, and resting during each focal watch (grazing time, playing time, and resting time respectively). In the case of the female, we calculated the number of time points (out of 30) that she spent in each of the recorded behaviors, providing information on grazing frequency, resting frequency and moving frequency.

Data were analyzed using linear and generalized linear mixed models using the packages lme4 (Bates et al. 2015) and glmmADMB (Skaug et al. 2006) in R version 3.1.3 (R Development Core Team 2008). All models included individual identity and the date on which the observation was conducted as random effects. They also included year (two level factor), maternal age (covariate) and lamb age (covariate) as fixed effects. To understand how a female's home range quality (both lifetime and annual) influenced maternal care, we compared a subset of 10 models for each trait, that contained all combinations of the following fixed effects: a quadratic term for lamb age to determine if a nonlinear relationship was a better fit to the data, the mean percentage cover or absolute cover of *Holcus lanatus* to test for an effect of home range quality, a quadratic term for the mean percentage cover or absolute cover of *Holcus lanatus* (again to test for a nonlinear relationship), and a first-order interaction between lamb age and the mean percentage cover or absolute cover of *Holcus lanatus* to examine whether the relationship between a given behavior and home range quality varied with lamb age. Both lamb age and the mean percentage cover or absolute cover of *Holcus lanatus* were mean centered and scaled to reduce collinearity between power terms. These models were compared using Akaike's Information Criterion corrected for small sample size (AICc). The best model was taken to be that with the lowest AICc value (Burnham and Anderson 2002); however, if there was a more parsimonious model (i.e. with fewer terms) that had a comparable AICc (<2 units difference) then the simpler model was accepted as the best model (Burnham and Anderson 2002). We present only the best model from each analysis in the results, but the outputs of full models and the AICc scores for full and best models are available in the supporting information (Tables S1-S4).

To understand if our results were affected by density variation within the study area we re-analyzed

the behavioral data using annual home range quality measures as above and the number of females with overlapping home ranges as an additional fixed effect. We used Bhattacharyya's affinity (BA) in adehabitatHR (Calenge 2006) to calculate the home range overlap/similarity for every pair of females that were alive and had more than five census observations in the year preceding each observation period. We then used this information to calculate the number of individuals whose utilization distribution had a BA exceeding 0.01 (BA scales from 0-1) with the utilization distribution of each behavioral female, at which point they were classed as having overlapping home ranges. For each trait we compared a set of 20 models that contained all possible combinations of the lamb age (linear and quadratic), home range quality (linear, quadratic, and first-order interaction with lamb age), and density terms. The best model was determined using AICc, as above. The results from these analyses were not qualitatively different to those from analyses excluding density and therefore they are presented in the supporting information (Table S2).

We used a similar approach when conducting analyses to understand whether maternal care behavior varied with habitat selection; however, in the place of the percentage cover of *H. lanatus*, we included PC1, PC2 and PC3. We therefore compared a subset of 54 models for each trait, that contained all combinations of the resource selection variables (PC1, PC2 and PC3), a quadratic term for lamb age, and a first-order interaction between each of the resource selection variables and lamb age. As for the analyses using home range quality metrics AICc was used to compare these models, with the best model taken to be that with the lowest AICc value unless there was a more parsimonious model with a similar AICc (<2 units difference) (Burnham and Anderson 2002). Because the estimates of resource selection functions are themselves associated with error, we wanted to understand whether this impacted the results of models performed using only the parameter estimates from the logistic regression used to estimate RSFs. To do this we used the parameter estimates and standard errors from the regressions for each individual to obtain a distribution from which we selected 100 random values. We then ran our mixed models using each of these set of values, deriving a best model from each (as above) to understand how many of these models - if any - featured any of the resource selection components.

Total sucking time (with and without failed suckling events), mean suckle duration (with and without failed suckling events), and grazing time were log transformed prior to analysis in order to ensure that the distribution of the residuals had a closer approximation to normality. These behaviors, along with resting time, were then analyzed using linear mixed models assuming a Gaussian

distribution. We assumed a Poisson distribution when analyzing suckling frequency (excluding failed suckling events), but used negative binomial mixed models (performed in glmmADMB) for suckling frequency (including failed suckling events), female grazing frequency, female resting frequency and female moving frequency due to the overdispersion apparent in the residuals when assuming a Poisson distribution. We assumed a binomial distribution when analyzing the proportion of successful suckling events, using the 'bobyqa' optimizer to aid convergence. We do not present results for playing time and the proportion of female terminated suckling events because severe zero-inflation resulted in poor residual distributions despite all transformations and error distributions employed.

To supplement the above analyses and aid in the interpretation of our behavioral results, we also investigated the effect of a female's annual home range quality on the growth of her lambs and her body condition at the end of the summer. Because only 39 lambs observed during 2014 and 2015 were caught in August catches (equating approximately to weaning), and the majority of these lambs were born to females with high quality home ranges (only seven lambs born to females with *H. lanatus* covers lower than 30%), we used data spanning the period 1985 to 2015 for this analysis. Similarly, we used data spanning the period 1988 to 2015 to maximize the sample size for body condition analyses. In order to be consistent with the behavioral work we restricted our analyses to females aged between three and eight years old, that had given birth to singleton lambs. This left us with 1079 lambs (born to 533 females) for growth analyses and 1168 females for the body condition analyses. We calculated lamb growth as the change in weight (in grams) between birth in April/May and the catch in August divided by the number of days between birth and August weight measurements, and maternal body condition as the residuals from a linear regression of August body mass against hind leg length. There has been substantial debate over the accuracy of this measure of body condition (Green 2001; Schulte-Hostedde et al. 2005); however, due to data limitations we are unable to use more direct measures of condition. Both lamb growth and body condition were analyzed using linear mixed effects models using lme4 (Bates et al. 2015). In both cases, maternal identity was included as a random effect, with lamb year of birth included as a random effect in growth models, whilst the year of measurement was included as a random effect in models of maternal body condition. In lamb growth models, we included the lamb's sex, maternal age, and julian birth date as fixed effects, whereas in maternal body condition models we included only the female's age as a fixed effect. To test for an association between home range quality and both lamb growth and female body condition, we then compared these models with a model that also contained the percentage cover of *H. lanatus* in a female's annual home range as a fixed effect and

another model containing a quadratic term for the mean annual home range percentage cover of *H. lanatus*. In both cases, we used home ranges calculated for the year preceding the lamb's birth. These models were also compared using AICc, with the best model taken to be that with the lowest AICc unless there was a more parsimonious model with a comparable AICc.

Results

Variation in home range quality

There was substantial between-individual variation in home range quality and habitat selection. Mean percentage covers of *H. lanatus* in female lifetime home ranges varied from 9.6% to 61.5%, with a similar pattern evident for annual home ranges, which had mean *H. lanatus* covers ranging from 10.2% to 64.3%. In the case of resource selection functions, there was considerable variation in the selection for the three broad community types (represented by the three principal components). The greatest variation was apparent in PC1 with beta coefficients for this principal component ranging from -12.8 to 1.0. In this case, the more negative the value, the greater the selection for plant species associated with grassland rather than species associated with heathland. The ranges for PC2 and PC3 were smaller than for PC1 but similar to each other at -0.1 to 9.6 and -0.8 to 9.9, respectively. In the case of PC2, more positive values corresponded to greater selection for species associated with HA grassland relative to *Festuca-Plantago* swards, whilst for PC3, more positive values were associated with greater selection for areas rich in *Calluna vulgaris*.

Lamb behaviors

Likelihood ratio tests of models with and without the individual identity random effect indicated that there was between individual variation in suckling frequency [with ($\chi^2(1) = 5.34$, p = 0.02) and without failed suckling events ($\chi^2(1) = 67.65$, p = < 0.0001)], mean suckle duration (without failed suckling events - $\chi^2(1) = 14.07$, p = 0.0002), suckling success ($\chi^2(1) = 6.00$, p = 0.01) and grazing time ($\chi^2(1) = 5.45$, p = 0.02) even when fixed effects were accounted for. As expected, lamb age was a key predictor in models for all the lamb behaviors recorded over the period of maternal care, being present in the best fit model in all cases (Table 2). This suggests that our methods were effective in capturing variation in lamb behaviors over this period. All of the measures of sucking behavior, as well as the total time a lamb spent resting, decreased as the lamb approached weaning (Table 2). However,

these relationships were non-linear, with the reduction being most pronounced within the first weeks of life (Fig. 1). In contrast, the total time a lamb spent grazing during each observation increased as they approached weaning, though after around 70 days of age the total time a lamb spent grazing decreased slightly (Table 2).

We first used lifetime home range quality metrics in our analyses as the females in our study were selected based on this measure. We found no evidence for a significant association between any of the measures of sucking behavior and the lifetime mean percentage cover of *H. lanatus* in a female's home range. Home range quality did not feature in the best fit model for any of the measures of lamb sucking behavior (Table 2), and this result was consistent whether failed suckling events were excluded or not (Table S3). We also found no evidence for a significant relationship between a female's home range quality and any of the non-suckling behaviors recorded, with home range quality absent from the best fit models for both grazing time and resting time (Table 2).

When we used the annual home range quality metrics we also found that the mean percentage cover of *H. lanatus* was not important in explaining any of the lamb behaviors studied (Table 2). As for the analyses using lifetime home range quality metrics, the mean percentage cover of *H. lanatus* in a female's annual home range did not feature in the best fit models for suckling frequency, mean suckle duration, suckling success, total sucking time, total grazing time, or total resting time (Table 2). Furthermore, the results for the suckling behaviors were consistent whether failed suckling events were included or not (Table S3). We also found that our results were equivalent when the absolute cover of *H. lanatus* in a female's home range was used, with this term absent from the best fit models for all lamb behaviors (Table S2).

Analyses using resource selection function coefficients tended to produce similar results to analyses performed using home range quality metrics, with none of the three coefficients (PC1, PC2, or PC3) featuring in best fit models for suckling frequency, mean suckle duration, total grazing time or total resting time (Table 2). These results were also consistent when failed suckling events were excluded (Table S3). In addition, when we performed models using resource selection coefficients that incorporated the error around the RSF parameter estimates our results were similar, with only 12 out of the 100 best fit models including any of the RSF coefficients. The one difference between the results of home range quality and RSF analyses came from models of suckling success. Suckling success was not explained by home range quality, whether lifetime or annual (Table 2). In contrast, when resource selection coefficients were used, both PC1 and PC3 featured in the best fit model for the proportion

of successful suckling events in first-order interactions with lamb age. These terms indicated that the relationship between suckling success and a female's habitat selection changed as the lambs aged (Table 2). When the lambs were young, there was little difference in suckling success with a female's selection for HA grassland; however, as the lambs approached weaning, individuals born to females exhibiting greater selection for heathland (communities dominated by *C. vulgaris*, *N. stricta* etc) had greater suckling success (Fig. 2). Similarly, as lambs aged, individuals born to females that selected for plant communities rich in *Calluna vulgaris* had greater suckling success (Table 2).

Female behaviors

We also found that female behaviors varied with lamb age, with grazing frequency declining with lamb age and both resting frequency and moving frequency increasing with lamb age (Table 3). As for lamb behaviors, there was no evidence for consistent variation in female behavior with home range quality. The mean percentage cover of *H. lanatus* in a female's lifetime home range did not feature in the best fit model for grazing frequency, moving frequency or resting frequency (Table 3). The same was generally true when we used annual home range quality metrics. Both the annual mean percentage cover of *H. lanatus* and annual absolute cover of *H. lanatus* were absent from the best fit models for all the female behaviors studied, except in the case of movement frequency when the number of overlapping females was included (Table 3 and Table S2). When the density term was included the absolute cover of *H. lanatus* featured in the best fit model, suggesting that females with higher quality home ranges spent more time moving per hour of observation (Table S2). Our results were also largely comparable when we used coefficients from individual resource selection functions in place of home range quality metrics, with none of the three principal components featuring in the best fit models for grazing frequency or resting frequency (Table 3). The results for moving frequency did differ slightly when using the resource selection coefficients, with PC2 featuring in the best fit model in a first order interaction with lamb age (Table 3). This term indicated that females who selected more highly for *Festuca-Plantago* swards spent more time moving.

Lamb growth and maternal body condition

Lamb growth between birth and August varied with both birth date and sex, with late born lambs and male lambs growing more quickly over this period (Table 4). However, there was no indication that lamb growth varied in relation to the quality of their mother's home range in the year preceding

their births as this term was not included in the best fit model (Table 4). There was also no indication that the quality of a female's home range in the year preceding the birth of her lamb affected her body condition in the following August (Fig. S4). The AICc of the model including home range quality (both linear and quadratic term) was equivalent (<2 unit difference) to the best model (selected following rules of parsimony); however, it was apparent from this model that the relationship between home range quality and female body condition was very weak (Fig. S4).

Discussion

In this study, we examine the role of individual-level, as opposed to population-level, variation in resource availability on post-natal maternal care in a wild-living mammal. We found no evidence that variation in female or lamb behavior over the period of maternal care was associated with variation in the quality of the home range occupied by a female Soay sheep. There was no indication that suckling frequency, or the mean duration of suckles varied with home range quality, and consequently there was no significant relationship between the quality of a female's home range and the total time her lamb spent sucking. There was also no indication that the quality of a female's home range influenced her lamb's grazing and resting behavior. Similarly, we found no association between either lifetime or annual home range quality and female grazing, resting or movement frequency. Our behavioral results were supported by our analyses of lamb growth, where we found that the quality of a female's home range had no influence on the weight gain of her lambs between birth and weaning. This also suggests that lambs born to females with home ranges of differing qualities did not receive differing levels of investment. In addition to providing comparable levels of care, females were in similar condition in the August following the birth of their lamb despite having home ranges of differing qualities. This may explain why a previous analysis found no apparent relationship between home range quality and female lifespan (Regan et al. 2016).

Though it is somewhat surprising that Soay sheep females do not adjust their investment into maternal care given the quality of their home range, we feel our results are robust for the following reasons. First, our sample size of 69 individuals is large relative to that of many similar studies using wild populations (e.g. Tremblay et al. 2004 - 26 individuals, Robertson et al. 1992 - 44 females with singletons, and Andersen et al. 2000 - 24 individuals). Second, by observing each female and her lamb over the entire period of maternal care, our results were not biased by examining the relationship between resource availability and care over a shorter time scale. Third, we recorded non-suckling behaviors both

of the female and the lamb, making it possible to examine whether the female or lamb adjusted such behaviors in response to the pattern of care. Finally, although the characterization of the resources available to an individual is complex, our results were robust across different measure of resource use, suggesting that resource variation was accurately captured. When using coefficients from RSFs, we found an association between female movement frequency and resource use that was not apparent in analyses using *H. lanatus* cover. This result suggests that females who select for *Festuca-Plantago* dominated swards moved more frequently during observations. It is not particularly surprising that we did not detect this trend with models using only *H. lanatus* covers as the amount of HA grassland in a female's home range is unlikely to correlate strongly with the amount of *Festuca-Plantago* sward within their home range, particularly as *Festuca-Plantago* swards are relatively restricted to the west of the study area. Individuals in these areas are also the least accustomed to human activity and as a result, are the most sensitive to human disturbance. It is therefore possible that this result is due to increased movements made by these individuals as a result of tourist disturbance.

Variation in resource availability is expected to alter the amount of parental care through its effects on the relative costs and benefits of parental care (Clutton-Brock 1991). Despite this, it has often proved difficult to demonstrate a link between resource availability and parental care behavior, as illustrated by our work and numerous other studies (e.g. Whittingham and Robertson 1994, Andrews et al. 2016). It seems unlikely that variation in resource availability would not affect the costs and benefits of parental care, but it is possible that this effect does not translate into the predicted difference in parental care behavior. In our case we can exclude any effects due to the behavior of a partner as only females provide care in this species. It is possible that behavioral measures of parental care may not accurately reflect the transfer of resources from parent to offspring. For instance, in the case of mammals, there is criticism surrounding the use of suckling behavior as an indicator of milk intake (summarised in Cameron (1998)) and maternal investment during lactation. For example, mothers may vary in the nutritional content of their milk, and offspring may therefore receive very different amounts of nutrition for the same amount of time spent sucking (Skibiel and Hood 2015). Furthermore, individual offspring may differ in the efficiency with which they obtain milk (Cameron 1998). Despite these concerns, we believe that our approach has characterized variation in parental care in Soay sheep. First, by observing individuals at various times throughout the day and across the entire maternal care period, it is unlikely that our results are biased due to within-day or seasonal variation in suckling behavior. Second, by measuring non-suckling behaviors of both a female and her lamb, we obtained

a more complete picture of each individual's decisions over this period. For example, by recording grazing behavior we were able to look for evidence of compensation by the female or her lamb for the level of parental care. Finally, because of the long-term nature of the St. Kilda Soay sheep project, we had access to a larger sample of growth data to validate any results from our behavioral observations. The results of this analysis confirm that variation in home range quality does not influence post-natal maternal care. This period includes a significant portion of time over which the lamb is able to supplement the nutrition gained from its mother by grazing, which may complicate any analysis of the relationship between home range quality and maternal care. Nevertheless, our results show that lamb grazing behavior does not vary with home range quality, supporting our suggestion that females with home ranges that differ in quality invest similarly into maternal care.

Our finding that environmental conditions have no effect on parental care has implications for our understanding of reproductive strategies in ungulates. Previous studies suggest that female ungulates tend to favor their own survival and reproduction over that of their offspring under poor conditions, thereby exhibiting a conservative reproduction strategy. For example, studies on bighorn sheep (*Ovis canadensis*) and white-tailed deer (*Odocoileus virginianus*) suggest that females exhibit bet-hedging strategies, such that there is little change in female mass/survival but there are significant reductions in offspring mass/survival when conditions are poor (Festa-Bianchet and Jorgenson 1998; Therrien et al. 2007; Martin and Festa-Bianchet 2010). In addition, other studies show that variation in forage quality between years or between populations is associated with behavioral differences or variation in offspring growth. For example, mountain goat (*Oreamnos americanus*) kids in Alberta, Canada, grow faster in years where forage quality is high (Côté and Festa-Bianchet 2001). Similarly, a recent study on Appennine chamois (*Rupicapra pyrenaica ornata*) found reductions in maternal care when pasture quality was poor (Scornavacca et al. 2016). Long-lived iteroparous species such as ungulates are expected to follow a conservative reproduction strategy, given that parents should favor their own reproduction when resource scarcity has a smaller impact on the future reproduction of the parent compared to that of the offspring (Clutton-Brock 1991). For this reason, we would also expect female Soay sheep to show such a pattern because their fitness is determined to a greater degree by their own survival and reproduction than that of offspring from any single litter (Clutton-Brock et al. 1996). However, in contrast to the above studies, we found no evidence that reduced home range quality altered the level of maternal care or the mass gain of lambs. Therefore, there was little evidence to suggest that female Soay sheep exhibit a conservative reproductive strategy in response to spatial

variation in resource availability.

One of the key reasons for why we did not find evidence for a conservative reproductive strategy in this study may lie in the specific biology of the St. Kilda Soay sheep. This population is characterized by instability, with periodic population crashes in which up to 70% of the animals on the island die (Clutton-Brock et al. 2004). Previous research suggests that Soay sheep females do not base decisions about reproductive investment upon information about future trends in population density, instead using information on current nutrition, body mass, and age (Marrow et al. 1996). Potentially, all females in our study were able to meet the costs of lactation regardless of the area in which their home range was located. Given that they were likely to be of high quality as heavier females are more likely to survive winter (Clutton-Brock et al. 1996), and that competition for vegetation during the summer is low due to the high productivity during this period (Crawley et al. 2004), all of our study females may have been able to counteract the costs of providing a high level of maternal care by consuming high quality resources during the high productivity period. Indeed, some studies using other systems have suggested that increased nutrient intake may be a cause for the absence of costs of reproduction (e.g. Hamel et al. 2009). The ability of the females to compensate for the costs experienced due to providing maternal care might explain why we did not detect any variation in lamb weight gain between birth and August given variation in female home range quality/resource selection, and why a previous study found no indication that lamb survival to weaning varied with the mean percentage cover of *H. lanatus* in a female's lifetime home range (Regan et al. 2016). Similarly, it may explain why lambs born to mothers with home ranges of higher quality have greater suckling success early in the season when vegetation is still limiting, whilst the opposite is true later in the summer when resource availability is high. This may indicate that females that differ in their use of space exhibit slightly different patterns of care over this period despite provisioning similarly over the total maternal care period. However, this result was driven partially by a lack of data for individuals with very negative PC1 and positive PC3 coefficients. Therefore to validate this interpretation, it would be necessary to study females that were more evenly distributed across the continuum of PC1 and PC3 values.

In both 2014 and 2015, twinning rates were low and we were therefore unable to include any twin litters in our sample. The reproductive costs of having a twins is likely to be greater than the costs resulting from having a singleton. As a result, the benefit of having a high quality home range may be more pronounced for females with twins. This is particularly pertinent given that, in many of the ungulate populations where conservative reproductive strategies have been illustrated, twinning

does not occur or is very rare [e.g. mountain goat (Côté and Festa-Bianchet 2001), bighorn sheep (Gaillard et al. 2000), chamois (Serrano et al. 2015)]. These studies may have been better capturing the behavior of individuals experiencing the greatest costs as a result of providing care. However, we feel that the lack of twins in our study is unlikely to be responsible for our results given that only the heaviest females give birth to twins (Clutton-Brock et al. 2004) and these individuals are likely to be able to better cope with the costs of providing care. Such a relationship may mean that an association between habitat use and maternal care provisioning would still be absent even if twin litters were included. Given the marked fluctuations in population density on St. Kilda, the conditions in the year when observations are conducted are likely to be important in determining the behavioral patterns observed. Indeed, the study by Robertson et al. (1992) showed that suckling behavior varies between years in St. Kilda Soay sheep. If we had conducted our observations in years where density in the previous winter had been low, the majority of individuals would have been in good condition in Spring, such that there would be little variation in the care they provide. This was not however the case, with high population density in the summer preceding both years of observation, at 545 individuals in the study area in the August of 2013 and 482 in the August of 2014. This is in contrast to recent lows of 362 and 335 in 2012 and 2002. We must consider the fact that variation in local density across the study area might have precluded an association between maternal care and home range quality, as higher density in areas of high quality might result in these areas being devalued. However, sheep consistently favor *Holcus-Agrostis* grassland, even when densities are high, potentially as a result of this community being more resilient to grazing pressure than other community types including wet and dry heath (Jones et al. 2005). Therefore, our result is unlikely to be entirely driven by variation in local density.

Our work adds to the existing literature on the effects of resource availability on parental care by examining the effect of spatial variation in resource availability quantified at the individual scale. In contrast, many of the previous studies have used resource availability estimates at the study area scale to study the effect of temporal variation in resources (e.g. Rachlow and Bowyer 1994 and Andersen et al. 2000), or have examined the effect of spatial variation in resource availability by estimating resource quantity/quality at scales above that of the individual home range (e.g. regions differing in the availability of nutritious pasture [Scornavacca et al. 2016]). Individuals are more likely to respond to the resource availability they experience in their home range than to the resources available in the study area or the area in which the population persists because it is the resource availability

at this scale that will determine the costs and benefits of care. Furthermore, different parts of a study area may vary in how the quantity/quality of resources varies over time, or indeed in more subtle fine-scale spatial patterns in resource availability. It is also likely that an individual's response to temporal variation in the environment, for example variation in density and weather conditions between years may be conditional on the environmental conditions it experiences on a within-year basis. We therefore feel that there is a need to conduct further studies based on the approach used in our study, which quantify resource availability at the individual scale in order to understand how environmental conditions influence the behavior of individuals. Movement ecology has provided the tools to quantify resource availability at the individual scale, and though the necessary data can be hard to come by we hope that the advance in tracking technologies, combined with reductions in the cost of using these technologies will make more studies of this kind possible.

In conclusion, we find that female Soay sheep vary substantially in their home range quality and in their selection for different plant communities, but there is nevertheless no evidence that home range quality influences their investment into maternal care, as indicated by both suckling behavior and estimates of lamb growth over the summer. There was no evidence that either the female or her lamb adjusted any of the non-suckling behaviors measured (such as grazing or resting). This suggests that females inhabiting areas of Village Bay with poorer vegetation did not compensate for the level of care they provided by for example spending a greater amount of their time grazing. Our study suggests that female Soay sheep with poorer quality home ranges do not maintain their own survival and reproduction at a cost to the survival of their lambs. We suggest that this is because females giving birth to a lamb in spring, particularly following high densities in the preceding winter, are in relatively good condition, and that resources are not limiting during the summer. This may mean that no matter where a female's home range is located, she is able to offset the costs of lactation by consuming additional resources. Our results demonstrate the need to examine the effect of resource variation quantified at the individual scale on individual reproductive investment decisions. Combining this approach with studies examining the effect of temporal variation in the environment on reproductive investment decisions may provide us with a more complete picture of the influence of resource availability on reproductive investment in natural populations.

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Data accessibility

Analyses reported in this article can be reproduced using the data provided by Regan et al. (2017).

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Table 1: Descriptions of the female and lamb behaviors recorded during focal observations

Individual	Behavior	Description
Lamb	Sucking	Recorded each time the lamb was in contact with the teat. The head is usually tilted upwards slightly and sucking is often accompanied by tail wagging and intense butting of the teat. Failed suckling events were classed as periods of suckling behavior that lasted less than five seconds. For each suckling event, termination by either the female or lamb was noted. Female termination was characterized by the female walking off or kicking the lamb, whereas lamb termination was noted when the lamb stopped sucking of its own accord.
Lamb	Grazing	Short periods of head down movement, but where lambs were explicitly seen taking bites of grass (in the first few days of life they show interest in grass but are yet to take it into their mouth).
Lamb	Resting	When the lamb is lying down.
Lamb	Playing	Either lone play or play involving other lambs, generally characterized by short bursts of running, leaping, and head butting.
Lamb	Other	A category for all behaviors that do not fit into the other described categories. It generally consists of movement behavior.
Lamb	Out of sight	This category was used to note periods when the lamb was not in view, whether this was because the lamb was obscured by an object, had gone out of sight during play, or had been disturbed in some way.
Female	Suckle	Noted when the female's behavior was recorded during a suckling bout.
Female	Grazing	Head down, taking bites and short periods of head down movement between bites.
Female	Resting	Female lying down and ruminating or showing no observable activity.
Female	Moving	If the female was showing any movement not associated with grazing.
Female	Other	Periods of activity that do not fit in the other described categories. Largely made up of grooming and general alertness.
Female	Out of sight	Used to denote periods when the female was not in view.

Table 2: Parameter estimates (± standard error) from the best fit models for all lamb behaviors (with and without failed suckling events), using lifetime home range quality estimates, annual home range quality estimates (A corresponds to the annual mean percentage cover of *H. lanatus*, whilst B corresponds to the annual absolute cover of *H. lanatus*) and annual resource selection function coefficients

Trait	Term	Lifetime home range		Annual home range A		Annual home range B		Resource selection function	
		Est(SE)	t/z*	Est(SE)	t/z*	Est(SE)	t/z*	Est(SE)	t/z*
Suckling frequency	Lamb age (days)	-1.09(0.06)	-19.76	-1.09(0.06)	-19.76	-1.09(0.06)	-19.76	-1.01(0.06)	-17.06
	Year (2015)	0.34(0.10)	3.56	0.34(0.10)	$3.7\times e^{-4}$	0.34(0.10)	3.56	0.31(0.11)	2.83
	Maternal age	-0.04(0.03)	-1.25	-0.04(0.03)	-1.25	-0.04(0.03)	-1.25	-0.04(0.03)	-1.26
	Lamb age^2	0.35(0.06)	5.36	0.35(0.06)	5.36	0.35(0.06)	5.36	0.34(0.07)	5.20
Mean suckle duration	Lamb age (days)	-0.35(0.05)	-7.16	-0.35(0.05)	-7.16	-0.35(0.05)	-7.16	-0.35(0.05)	-7.16
	Year (2015)	-0.03(0.08)	-0.35	-0.03(0.08)	-0.35	-0.03(0.08)	-0.35	-0.03(0.08)	-0.35
	Maternal age	0.03(0.02)	1.11	0.03(0.02)	1.11	0.03(0.02)	1.11	0.03(0.02)	1.11
	Lamb age^2	0.26(0.06)	4.54	0.26(0.06)	4.54	0.26(0.06)	4.54	0.26(0.06)	4.54
Sucking time	Lamb age (days)	-1.41(0.08)	-17.75	-1.41(0.08)	-17.75	-1.41(0.08)	-17.75	-1.43(0.08)	-17.55
	Year (2015)	0.36(0.13)	2.76	0.36(0.13)	2.76	0.36(0.13)	2.76	0.38(0.13)	2.86
	Maternal age	$-6.6\times e^{-4}$(0.04)	-0.02	$-6.6\times e^{-4}$(0.04)	-0.02	$6.6\times e^{-4}$(0.04)	-0.02	0.003(0.04)	0.07
	Lamb age^2	0.49(0.09)	5.74	0.49(0.09)	5.74	0.49(0.09)	5.74	0.51(0.09)	5.81
Suckling success	Lamb age (days)	-0.10(0.11)	-0.96	-0.10(0.11)	-0.96	-0.10(0.11)	-0.96	-0.005(0.12)	-0.04
	Year (2015)	-0.17(0.17)	-1.04	-0.17(0.17)	-1.04	-0.17(0.17)	-1.04	-0.11(0.17)	-0.67

	Maternal age	0.08(0.04)	1.74	0.08(0.04)	1.74	0.08(0.04)	1.74	0.09(0.05)	1.93
	Lamb age^2	0.39(0.13)	2.98	0.39(0.13)	2.98	0.39(0.13)	2.98	0.49(0.13)	3.63
	PC1	-	-	-	-	-	-	0.002(0.06)	0.04
	PC3	-	-	-	-	-	-	-0.06(0.10)	-0.61
	Lamb age:PC1	-	-	-	-	-	-	0.24(0.06)	3.79
	Lamb age:PC3	-	-	-	-	-	-	0.26(0.09)	2.80
Grazing time	Lamb age (days)	2.86(0.13)	21.84	2.86(0.12)	21.84	2.86(0.13)	21.84	2.86(0.13)	21.84
	Year (2015)	-0.04(0.23)	-0.19	-0.04(0.23)	-0.19	-0.04(0.23)	-0.19	-0.04(0.223)	-0.19
	Maternal age	-0.004(0.07)	-0.06	-0.004(0.07)	-0.06	-0.004(0.07)	-0.06	-0.004(0.07)	-0.06
	Lamb age^2	-1.66(0.14)	-11.79	-1.66(0.14)	-11.79	-1.66(0.14)	-11.79	-1.66(0.14)	-11.79
Resting time	Lamb age (days)	-332.29(57.97)	-5.73	-332.29(57.97)	-5.73	-332.29(57.97)	-5.73	-332.29(57.97)	-5.73
	Year (2015)	-80.95(88.02)	-0.92	-80.95(88.02)	-0.92	-80.95(88.02)	-0.92	-80.95(88.02)	-0.92
	Maternal age	12.10(27.61)	0.44	12.10(27.61)	0.44	12.10(27.61)	0.44	12.10(27.61)	0.44
	Lamb age^2	150.88(62.51)	2.41	150.88(62.51)	2.41	150.88(62.51)	2.41	150.88(62.51)	2.41

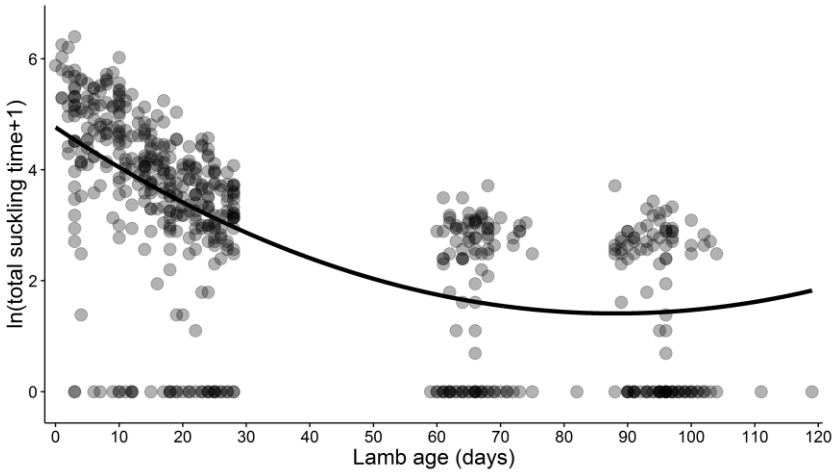
* t values are reported for linear mixed effects models whilst z values are reported for generalised linear mixed effects models.

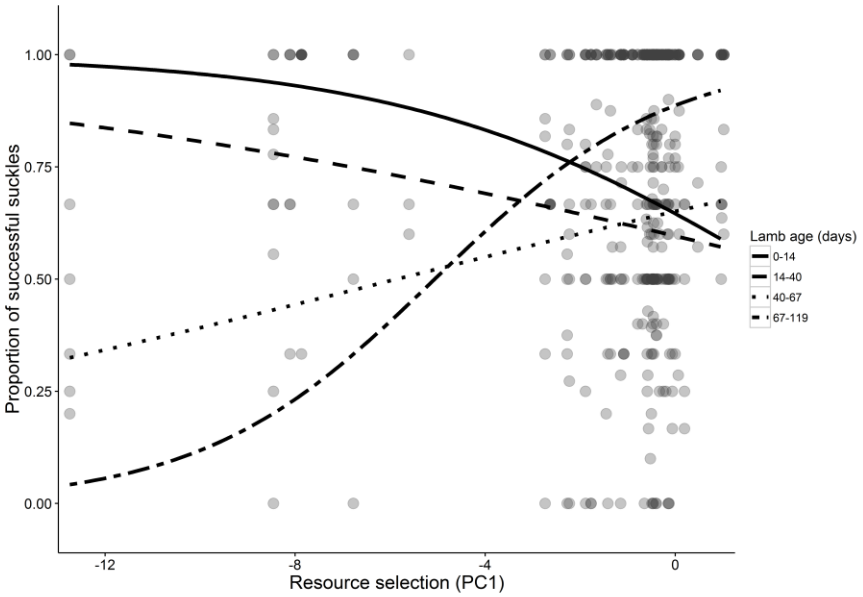
Table 3: Parameter estimates (± standard error) from best models for all female behaviors, using lifetime home range quality estimates, annual home range quality estimates (A corresponds to the annual mean percentage cover of *H. lanatus*, whilst B corresponds to the annual absolute cover of *H. lanatus*) and annual resource selection function coefficients

Trait	Term	Lifetime home range		Annual home range A		Annual home range B		Resource selection function	
		Est(SE)	z	Est(SE)	z	Est(SE)	z	Est(SE)	z
Grazing frequency	Lamb age (days)	-0.14(0.02)	-7.96	-0.14(0.02)	-7.96	-0.14(0.02)	-7.96	-0.14(0.02)	-7.96
	Year (2015)	0.06(0.03)	1.74	0.06(0.03)	1.74	0.06(0.03)	1.74	0.06(0.03)	1.74
	Maternal age	0.005(0.01)	0.48	0.005(0.01)	0.48	0.005(0.01)	0.48	0.005(0.01)	0.48
Resting frequency	Lamb age (days)	0.48(0.08)	5.79	0.48(0.08)	5.79	0.48(0.08)	5.79	0.48(0.08)	5.79
	Year (2015)	-0.43(0.17)	-2.57	-0.43(0.17)	-2.57	-0.43(0.17)	-2.57	-0.43(0.17)	-2.57
	Maternal age	-0.009(0.05)	-0.17	-0.009(0.05)	-0.17	-0.009(0.05)	-0.17	-0.009(0.05)	-0.17
Moving frequency	Lamb age (days)	0.11(0.06)	1.73	0.11(0.06)	1.73	0.11(0.06)	1.73	0.20(0.09)	2.34
	Year (2015)	0.43(0.17)	2.48	0.43(0.17)	2.48	0.43(0.17)	2.48	0.47(0.17)	2.68
	Maternal age	-0.02(0.05)	-0.47	-0.02(0.05)	-0.47	-0.02(0.05)	-0.47	-0.04(0.05)	-0.84
	PC2	-	-	-	-	-	-	-0.10(0.06)	-1.65
	Lamb age:PC2	-	-	-	-	-	-	0.08(0.05)	-1.59

Table 4: Parameter estimates (± standard error) for full and best models of lamb growth (between birth and weaning) and maternal body condition. In both cases home range qualities were derived from annual home ranges

	Term	Full model		Best model	
		Est (SE)	t	Est (SE)	t
Lamb growth	Maternal age	0.13(0.26)	0.48	0.12(0.26)	0.48
	Sex (male)	14.43(0.80)	18.02	14.43(0.80)	18.02
	Birth date	0.57(0.09)	6.41	0.57(0.09)	6.50
	HR quality	-0.06(0.22)	-0.26	-	-
	HR quality^2	$7.8\times e^{-4}$(0.003)	0.27	-	-
Maternal body condition	Maternal age	0.20(0.03)	7.36	0.20(0.03)	7.32
	HR quality	-0.03(0.07)	-0.41	-	-
	HR quality^2	-0.10(0.06)	-1.62	-	-


ln(total suckling time+1)
0
2
4
6
0
10
20
30
40
50
60
70
80
90
100
110
120
Lamb age (days)


1.00
0.75
0.50
0.25
0.00
Proportion of successful suckles
-12
-8
-4
0
Resource selection (PC1)
Lamb age (days)
0-14
14-40
40-67
67-119